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Optimal tempo and defence for consumers of multiple resources

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ABSTRACT

Ecological models of behaviour are typically based on the assumption that decisions can be evaluated with a single resource currency. Here we present models that predict the tactics of consumers collecting two nutritionally distinct resources: fuel that is used for activity and food used for growth (F4G). Both models assume that foragers seek to maximize F4G gain subject to collecting enough fuel for activity. Our first model determines the optimal tempos of foraging for each resource. While foraging for fuel, consumers use and collect the same resource and optimal behaviour is identical to the predictions of a single resource model. However, because consumers use fuel to acquire F4G, they are predicted to work harder to acquire F4G when fuel is more available. Our second model examines how consumers should allocate their time among foraging for fuel, foraging for F4G and defence of F4G sources. Optimal investment in defence increases when fuel is available (because expenditures can be quickly recovered) and when F4G is scarce (because fewer opportunities exist for obtaining new sources of F4G). Our results suggest that behaviours will appear wasteful when foraging environments are fuel-rich and overly frugal when F4G is common but fuel is scarce.

Keywords: defence, optimal foraging, provisioning, tempo.

INTRODUCTION

To make foraging theory experimentally tractable, energy gain is often assumed to serve as a surrogate currency for fitness (Stephens and Krebs, 1986; McNamara and Houston, 1997). Energy currencies provide several advantages: they are practical because the energetic gains and expenses of activities can be measured and compared, and they are widely applicable because all food items contain energy and all metabolic processes consume it (Calow and Townsend, 1981). However, researchers have long recognized that the diversity of food chemistry and the complexities of animal nutrition can often restrict the applicability of foraging models based solely on energy gain (Pulliam, 1975; Belovsky, 1978; Rapport, 1980). Foods contain different combinations of protein, carbohydrates, lipids and other nutrients, and animals need an appropriate quantity and mixture of these nutrients for

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maximal performance (Raubenheimer and Simpson, 1997). Thus, to obtain a nutritionally balanced diet, foragers might often seek foods that are energy-poor but contain nutrients that are scarce or in high demand (Cottam, 1985; Pennings *et al.*, 1993).

Food chemistry may also affect foraging decisions through its influence on resource allocation. Allocation models are frequently based on the assumption that energy is equally suitable for meeting any of an animal's demands (Stearns, 1992; Perrin and Sibly, 1993). However, different characteristics often need distinct mixtures of nutrients; for instance, activity can be fuelled with energy from carbohydrates or lipids, while tissue production requires a diversity of materials, including protein (Dadd, 1985). Because of these distinct requirements, the relative sizes of different nutrient pools may affect the relative costs of demands. As a result, the chemical composition of available resources may influence the behavioural decisions that are contingent on these costs.

In this paper, we analyse tempo (rate of work) and territorial defence for organisms that collect two distinct resources: fuel and food for growth (F4G). We assume that fuel serves as a substrate for energy metabolism, while F4G has the particular mixture of nutrients needed for tissue production. In one version (the pure food model), we assume that consumers obtain these resources from different foods, such as when omnivores collect carbohydrate-rich nectars or fruits and protein-rich pollen or animal tissue. In a second version (the mixed food model), we investigate the responses of consumers that specialize on one food that contains both fuel and F4G. Success in the models is determined by the rate of F4G gain subject to the forager collecting sufficient fuel to meet its metabolic requirements.

In our first model, we investigate foraging tempo. Tempo has received little attention in optimal foraging theory. Parameters affecting tempo, such as travel speed and feeding rate, are held constant in classical foraging theory (Stephens and Krebs, 1986) and relatively few models consider these parameters explicitly (Ware, 1975; Pyke, 1981; Ydenberg *et al.*, 1994; Hedenström and Alerstam, 1995; Shaw *et al.*, 1995). Because these models use energy-based currencies, theoretical work has not examined the influence of nutritional demands on rates of foraging activity.

Variation in tempo has been studied primarily in social insects (Oster and Wilson, 1978; Franks, 1985; Leonard and Herbers, 1986; Dyer and Seeley, 1991; Davidson, 1997). Oster and Wilson (1978) noted that 'workers of some ant species walk slowly and with seeming deliberation', whereas workers of other species 'literally seethe with rapid motion. [They] appear to waste substantial amounts of time canceling one another's actions' (pp. 281–282). Oster and Wilson (1978) assumed that high tempo increases productivity by increasing rates of resource discovery and acquisition, but also exposes workers to greater risks. They reasoned that tempo may increase with resource abundance and colony size because resource-rich environments provide ample opportunities for finding new prey items and large colonies can absorb higher rates of worker loss.

Davidson (1997) proposed alternatively that variation in ant tempo might be explained by differences in dietary ratios of carbohydrates and protein. She suggested that ants with carbohydrate-rich diets may have carbohydrates in excess of those required for growth and reproduction: ants could then use this excess to subsidize high tempo at little or no cost. It is this hypothesis that inspired us to develop the tempo model presented below.

Davidson (1997) also suggested that ants with excess carbohydrates might be more pugnacious, because these resources can also be used for territorial defence. We explore this hypothesis in our second model, which examines the trade-off between foraging and territorial defence for a consumer of fuel and F4G. We define territorial defence as

any activity that indirectly increases the consumer's rate of F4G acquisition. Although territorial defence has numerous meanings in the literature (Maher and Lott, 1995), here we refer to it only in terms of its consequences for foraging. Several models have investigated resource-based trade-offs between foraging and defence (e.g. Davies and Houston, 1981, 1984; Kacelnik *et al.*, 1981); however, the model presented here is the first to consider how multiple resource inputs influence the outcome of these trade-offs.

THE TEMPO MODEL

To organize our results, we present four versions of the tempo model. In the first version, foragers collect only energy and seek to maximize net energy gain; it is thus a classical optimal foraging model. In the second version, foragers again collect energy, but here they use it both to feed themselves and to provision their offspring. This version makes the same basic assumptions as some previous models of provisioning, including those of Ydenberg *et al.* (1994), Houston (1995) and Hedenström and Alerstam (1995). In the final two versions, foragers collect both fuel and F4G that are found in distinct sources (the pure food model) or are combined in a single resource (the mixed food model).

Energy model

In this version, organisms must choose a tempo S_e that maximizes the net rate at which they acquire energy (Table 1 summarizes our notation). We assume that tempo increases the rate of energy acquisition with diminishing returns and linearly increases foraging costs. The energy collection rate is

$$P = \frac{a_e S_e}{1 + k_e S_e} - c_e S_e \tag{1}$$

Table 1. Symbols used and their definitions (parameter values used in the examples are in parentheses)

Model	Symbol	Definition
Tempo	S_e, S_n	Tempo of foraging
	T_e, T_n	Fraction of time spent on an activity
	a_e, a_n	The slope of the relationship between resource gain and tempo at low tempo
	k_e, k_n	The extent of diminishing returns on resource gain with higher tempo (0.25, 0.25)
	c_e, c_n	The slope of the relationship between fuel use and tempo (0.25, 0.25)
	q	Fraction of a mixed food consisting of fuel
Territorial defence	T_e, T_n, T_d	Fraction of time spent on an activity
	b_e, b_n	Rate of resource gain
	m_e, m_n	The slope of the relationship between defence and rate of resource gain (20, 20)
	$\bar{b}_e$, $\bar{b}_n$	Rate of resource gain without defence
	c_e, c_n, c_d	Rate of fuel use during an activity (2, 2, 3)
	q	Fraction of a mixed food consisting of fuel

The parameter a_e represents the slope of the relationship between energy acquisition and tempo at low tempo, and is thus a measure of the availability of resources. The parameter k_e describes the diminishing returns on acquisition, while c_e represents the cost of increasing tempo.

We can find the optimal tempo by differentiating P with respect to S_e and setting the result equal to 0. This optimum is

$$S_e^* = \frac{1}{k_e}\left(\sqrt{\frac{a_e}{c_e}} - 1\right) \qquad (2)$$

Optimal tempo becomes larger as resources become more available (larger a_e), the extent of diminishing returns becomes less severe (smaller k_e) or the cost of foraging decreases (smaller c_e). The rate of energy collection with the optimal tempo is

$$P^* = \frac{(\sqrt{a_e} - \sqrt{c_e})^2}{k_e} \qquad (3)$$

Finally, the efficiency, total resource intake divided by cost, is

$$\frac{\text{intake}}{\text{cost}} = \sqrt{\frac{a_e}{c_e}} - 1 \qquad (4)$$

Provisioning model

In the provisioning version, organisms seek to maximize the energy they provide to their offspring by choosing an optimal tempo S_e and an optimal fraction of time T_e to spend foraging for themselves (with the remaining time T_n spent acquiring provision). The amount of energy delivered to offspring is

$$P = \frac{a_e S_e}{1 + k_e S_e}(1 - T_e) \qquad (5)$$

subject to the constraint

$$F: \frac{a_e S_e}{1 + k_e S_e} T_e = c_e S_e$$

which ensures that the provisioner meets its own requirements for energy.

Substituting the constraint into equation (4) gives

$$P = \frac{a_e S_e}{1 + k_e S_e} - c_e S_e \qquad (6)$$

which is identical to the objective in the energy model. The energy model and provisioning model thus predict the same optimal tempo because, in each case, the organisms seek to maximize the excess energy collected in a given amount of time. Because the optimal

tempos are the same, the efficiency of provisioning, defined as provision delivered divided by cost of collection, or

$$\frac{\text{provision delivered}}{\text{cost}} = \sqrt{\frac{a_e}{c_e}} - 1 \tag{7}$$

is also the same as the efficiency predicted by the energy model. However, the provisioning model also describes the amount of time T_n spent foraging for provision, and can be solved as

$$T_n = 1 - \sqrt{\frac{c_e}{a_e}} \tag{8}$$

Organisms should spend more time provisioning when energy is widely available (high a_e) or foraging is not costly (low c_e).

Fuel and F4G models

In the fuel and F4G versions, we assume that organisms use fuel immediately to fund foraging costs, with the goal of maximizing F4G acquisition. We present two models with different assumptions about how resources are packaged: a pure food model and a mixed food model.

Pure food model

In this model, we assume that organisms obtain fuel and F4G from different foods. As in the provisioning version, organisms must choose an optimal tempo S_e for foraging for fuel. They must also spend an optimal fraction of time T_e foraging for fuel (the remaining fraction of time T_n is spent foraging for F4G). In addition, organisms must choose an optimal tempo S_n for foraging for F4G. The amount of F4G acquired by an organism is

$$P = \frac{a_n S_n}{1 + k_n S_n} T_n \tag{9}$$

where a_n and k_n represent the availability of F4G and the extent of diminishing returns, like a_e and k_e. This payoff is subject to two constraints

$$F_1 : \frac{a_e S_e}{1 + k_e S_e} T_e - c_e T_e S_e - c_n T_n S_n = 0$$

$$F_2 : T_e + T_n = 1$$

representing, respectively, the energy constraint and the time constraint. The parameter c_e is the cost of increasing the tempo of foraging for fuel, and c_n is the cost of higher tempo during foraging for F4G.

To find the optima, we use the method of Lagrange multipliers for maximizing a multivariate function with constraints. We find that S_e in this version takes on the same

value as in the energy and provisioning models (equation 2) because it maximizes the net rate of fuel intake. The optimal tempo for collecting F4G is

$$S_n^* = \sqrt{\frac{P^*}{c_n k_n}} \tag{10}$$

where P^* is the rate of fuel collection at optimal tempo, as defined in equation (3). The time spent foraging for F4G is

$$T_n = \frac{1}{1 + \sqrt{\frac{c_n}{k_n P^*}}} \tag{11}$$

Note that the availability of F4G (a_n) has no effect on either the optimal tempo or the optimal duration of foraging for F4G. These solutions also predict that the tempo and duration of foraging for F4G should increase when foraging for fuel is more profitable.

The efficiency, here defined as F4G gain divided by energy cost, is

$$\frac{\text{F4G}}{\text{cost}} = \frac{a_n}{\sqrt{a_e c_n}} \tag{12}$$

Mixed food model

In this model, organisms collect one food type, a fraction q of which consists of fuel with the remaining $1 - q$ consisting of F4G. Organisms must choose the tempo, S, that maximizes the rate at which they acquire F4G. The amount of F4G collected by the organism is

$$P = \frac{(1 - q)aS}{1 + kS} \tag{13}$$

Collecting F4G is subject to a constraint on fuel use

$$\frac{qaS}{1 + kS} - cS = 0$$

where c is the cost of foraging. Organisms maximize F4G intake by foraging at the maximum tempo that satisfies the fuel constraint,

$$S^* = \frac{q\frac{a}{c} - 1}{k} \tag{14}$$

The efficiency, computed as F4G collected per unit cost, is

$$\frac{\text{F4G}}{\text{cost}} = \frac{1 - q}{q} \tag{15}$$

The results of the pure and mixed food models make several predictions about the behaviour of organisms collecting F4G. First, access to fuel increases the amount of effort a

forager can invest in F4G acquisition. In the pure food model, the optimal tempo and duration of foraging for F4G increase when foraging for fuel is more profitable. How fuel profits should be allocated between tempo and the duration of foraging for F4G depends on k_n, the extent to which higher tempo diminishes returns (when k_n is higher, S_n decreases and T_n increases). In the mixed food model, optimal tempo increases when forage is richer in fuel.

Second, when organisms collect F4G, their tempo need not maximize any single currency such as net energy gain (Fig. 1). Because fuel is used to collect F4G, the costs and benefits of foraging for F4G cannot be combined into a simple currency and a direct comparison of fuel use and F4G gain will not yield the optimal solution.

Third, foragers should use fuel less efficiently to collect F4G when the ratio of fuel to F4G availability is higher – that is, when the ratio of availabilities ($a_e : a_n$) increases in the pure food model or when forage in the pure food model contains more fuel (higher q). Because investment in foraging for F4G is determined by net fuel gain and is not affected by F4G availability, omnivores with easy access to fuel sources and specialists on fuel-rich resources should spend more effort acquiring F4G, even when returns diminish. As a result, optimal tempo in the fuel and F4G models increase relative to those predicted by the energy model as the ratio of fuel to F4G availability increases (Fig. 2). Thus, tests of tempo models with an energy currency will conclude that foragers are wasteful if foragers are using easily accessible fuel resources to obtain scarce F4G or if they are collecting fuel-rich resources. Similarly, when the ratio of fuel to F4G availability is low, optimal tempo while foraging for

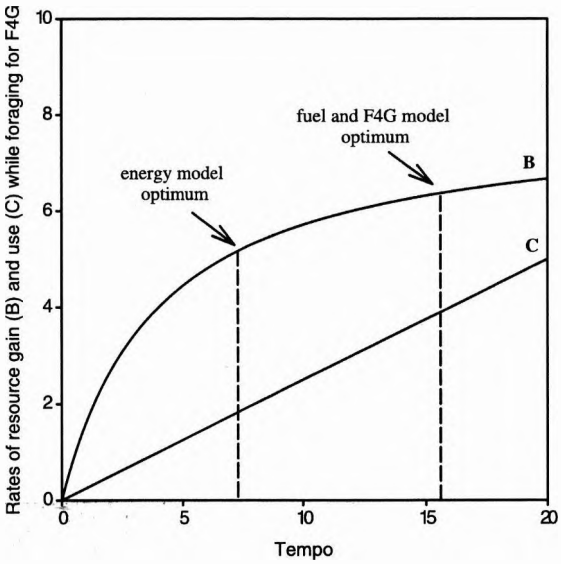

Fig. 1. The relationship in the pure food model between tempo and the rates of resource gain and use while foraging for food for growth (F4G). In an energy version of the model, optimal tempo would maximize the difference between these rates. In the fuel and F4G version, the predicted tempo may be different from this energetic optimum because rates of resource use are influenced by the profitability of foraging for fuel. The parameter a_e, which describes the relationship between resource gain and tempo at low tempo and is a measure of fuel availability, is three times, a_n, the availability of (F4G) in this example. All other parameter values are given in Table 1.

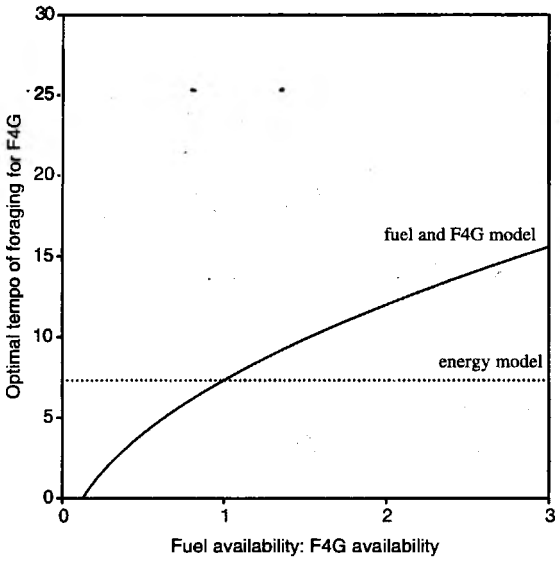

Fig. 2. Optimal tempo of foraging for F4G predicted by the pure food version of the fuel and F4G model, and the tempo predicted by the energy model, as functions of the ratio of fuel to F4G availability. We use $a_e : a_n$, the ratio of fuel to F4G gain at low tempo, to indicate the ratio of fuel to F4G availability (another measure of relative availability, the ratio of the diminishing return parameters $k_e : k_n$, produces similar results). Other parameter values are as in Fig. 1.

F4G is lower than the solution that maximizes net energy gain, and thus foraging behaviour will appear overly frugal.

THE TERRITORIAL DEFENCE MODEL

Our second set of models determines how organisms should allocate their time between foraging and territorial defence. We define territorial defence as any activity that increases indirectly a consumer's rate of F4G acquisition. Defending could thus include such activities as protecting F4G patches, which would increase the length of time that a forager can hold exclusive access to food finds, and patrolling foraging areas, which would increase the number of local F4G patches that the forager can discover before its competitors.

We present two versions of the model: an energy version and a fuel and F4G version. In both versions, we assume that the costs of foraging and defending are constant and thus the tempos of activities are fixed. To simplify presentation, we also assume that defending increases resource acquisition rates at a constant rate. A more complicated version with non-linear benefits of defence does not qualitatively alter the main results (unpublished results).

Energy model

In this version, organisms seek to maximize their net gain of energy by choosing an optimal fraction of time T_d to spend defending (with the remaining time T_e spent foraging for energy). The rate of energy acquisition is

$$b_e = m_e T_d + \bar{b}_e \tag{16}$$

The parameter m_e is the effect of defence on the rate of energy acquisition, and $\bar{b}_e$ is the energy acquisition rate without defence (a measure of the availability of energy). The payoff is the energy collected, or

$$P = T_e b_e \tag{17}$$

which is subject to an energy constraint and a time constraint

$$F_1 : T_e b_e - T_e c_e - T_d c_d = 0$$

$$F_2 : T_e + T_d = 1$$

The parameters c_e and c_d are the rates of fuel use while foraging for fuel and while defending, respectively.

Using the method of Lagrange multipliers, we find that the optimal time spent defending is

$$T_d = \frac{1 + c_e - (1 + c_d)\dfrac{\bar{b}_e}{m_e}}{2 + c_e + c_d} \tag{18}$$

In this version, the optimal investment in defence decreases when resources are more widely available (higher $\bar{b}_e$). The model also predicts that defence will increase when foraging for energy is expensive (higher c_e) and when defence is effective (higher m_e) or cheap (lower c_d).

Fuel and F4G models

In these models, organisms use fuel to fund all of their activities and the optimal strategy maximizes the acquisition of F4G. As in the fuel and F4G models of tempo, we present two versions that make different assumptions about how resources are packaged.

Pure food model

In this version, organisms acquire fuel and F4G from different foods. They must choose optimal fractions of time for foraging for fuel T_e and for defending T_d (with the remaining time T_n spent foraging for F4G). For simplicity, we assume that defending increases only the rate of F4G gain, b_n; the rate of fuel gain, b_e, is a constant in this model. The rate of F4G acquisition is

$$b_n = m_n T_d + \bar{b}_n \tag{19}$$

where m_n is the effect of defence on F4G gain and b_n is the availability of F4G. The amount of F4G acquired is

$$P = T_n b_n \tag{20}$$

The energy constraint and the time constraint are

$$F_1 : T_e b_e - T_e c_e - T_n c_n - T_d c_d = 0$$

$$F_2 : T_e + T_n + T_d = 1$$

where c_e, c_n and c_d are the rates of fuel use when organisms forage for fuel, forage for F4G and defend, respectively.

Again using Lagrange multipliers, we find that the optimal time spent collecting F4G is

$$T_n = \frac{b_e - c_e + (b_e - c_e + c_d)\dfrac{\bar{b}_n}{m_n}}{2(b_e - c_e + c_n)} \tag{21}$$

and the optimal time spent defending is

$$T_d = \tfrac{1}{2}\left[\frac{(b_e - c_e)}{(b_e - c_e + c_d)} - \frac{\bar{b}_n}{m_n}\right] \tag{22}$$

These equations make several predictions. First, organisms should spend more time foraging for F4G when fuel or F4G is more widely available (larger b_e or $\bar{b}_n$). Second, unlike in the energy version, here the optimal investment in defence *increases* when fuel is more widely available (larger b_e); it also increases when defending is cheaper (smaller c_d) and when it is more effective (larger m_n). Most importantly, allocation to defence should increase with the ratio of fuel to F4G availability (Fig. 3). As in the tempo model, the ratio of fuel to F4G availability affects the efficiency with which fuel is used to collect F4G. Comparing the investment in defence predicted by the fuel and F4G model to the level predicted by the energy model, we find that the fuel and F4G model predicts relatively higher levels when the ratio of fuel to F4G is high (Fig. 4). Thus, like the tempo of foraging for F4G, defence of F4G resources should appear wasteful when the environment is fuel-rich, and under-funded when fuel is scarce and F4G is more widely available.

Mixed food model

In the mixed food model, organisms collect one food that contains an amount, q, of F4G, with the remainder, $1 - q$, consisting of fuel. Organisms must choose an optimal fraction of time T_d to spend on defence, with the remaining time T_e spent foraging, to maximize the amount of F4G collected. Defence linearly increases the rate of food acquisition

$$b_e = m_e T_d + \bar{b}_e \tag{24}$$

where m_e is the effect of defence on food gain and $\bar{b}_e$ is the availability of food. Organisms are subject to a fuel constraint and a time constraint

$$F_1 : T_e b_e (1 - q) - T_e c_e - T_d c_d = 0$$

$$F_2 : T_e + T_d = 1$$

where c_e and c_d are the rates of fuel use while foraging for food and while defending, respectively. The optimal investment in defence in this model is the same as that predicted by the energy model.

DISCUSSION

Our fuel and F4G models examine how a consumer's relative access to different resources can influence its behavioural decisions. These simple models are based on a widely applicable assumption about nutrition – that consumers use different substrates for growth and activity. Although many optimal foraging models have investigated how nutrition

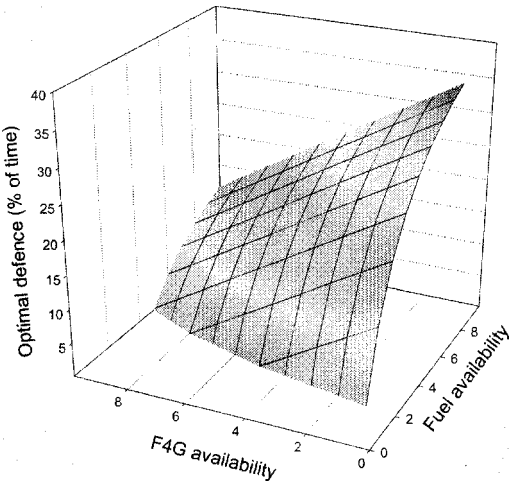

Fig. 3. Optimal defence as a function of the availabilities of fuel and F4G. Fuel availability is b_e, the rate of fuel acquisition; the availability of F4G is $\bar{b}_u$, the rate at which F4G is acquired without defence. Parameter values are given in Table 1.

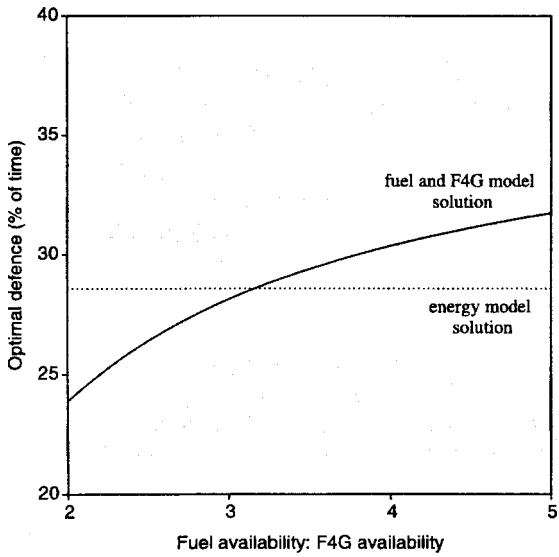

Fig. 4. Optimal defence in the energy version and the pure food fuel and F4G version of the territorial defence model as functions of the ratio of fuel to F4G availability. The ratio of fuel to F4G availability is indicated by $b_e : \bar{b}_u$, the ratio of fuel acquisition rate to the rate of F4G acquisition without defence. Parameter values are given in Table 1.

constrains diet choice, this work breaks new ground by concentrating instead on how nutrition constrains the resource use strategies that impinge on foraging decisions.

The tempo models predict that the efficiency of resource use during foraging will depend on the balance of available resources. Both the pure food and mixed food models predict

that organisms will forage for F4G at higher tempo when fuel is more abundant. Although working harder increases the rate of food gain, it also reduces the gain per unit of effort. However, when fuel is abundant, these diminishing returns are less important because the fuel used for activity is easier to replace. The energy version of the model also predicts that tempo will increase when fuel is more abundant. However, here it increases because there are more foraging opportunities to exploit, resulting in an *increase* in resource use efficiency in fuel-rich environments.

For territorial defence, the results of the fuel and F4G models depend on how the resources are packaged. In the pure food model, fuel-rich environments favour organisms that spend more of their time collecting or defending F4G. When F4G is scarce, fewer acquisition opportunities are lost when time is spent on defence. As a result, high ratios of fuel availability to F4G availability favour more defence and thus lower resource use efficiency. In contrast, the energy version of the model predicts lower defence (and higher efficiency) when fuel is more abundant because, under these conditions, more opportunities exist for directly obtaining resources and thus more opportunities are lost when time is diverted to defence. In the mixed food model, food composition (q), and thus the fuel to F4G availability ratio, does not affect optimal investment in defence. Instead, optimal defence equals the solution in the energy version because, like in the energy version, it depends on the opportunities lost when time is diverted from collecting a single resource.

It is interesting to contrast the predictions of our pure food defence model with the classic prediction that intermediate levels of energy availability favour defence (reviewed in Davies and Houston, 1984). Defence is predicted at intermediate levels of energy availability because, in an energy-poor environment, gains from defence do not cover the direct costs of the defence and, in a rich environment, too many opportunities for collecting energy are lost when time is spent defending (Carpenter and MacMillen, 1976; Carpenter, 1987). In a sense, these relationships are embedded in the solution for defence in our pure food model (equation 22). The ability to cover the direct costs of defence depends on the availability of fuel (b_e). Thus, low fuel availability favours less defence. On the other hand, opportunity costs increase with the availability of F4G ($\bar{b}_n$). Thus, *high* F4G availability favours less defence. These contrasting relationships are what produce the positive association between investment in defence and the ratio of fuel to F4G availability.

The predicted influence of fuel availability on strategies for obtaining growth-enriching food has two main implications for empirical studies. First, it implies that no single resource currency will serve as a general fitness surrogate when the benefits of behaviours are not solely energy-based. Surrogate currencies, such as the net rate of energy intake, energetic efficiency and energy use efficiency (food gain/energy used), evaluate behaviours by comparing the rates at which resources are used and gained during an activity. Our models suggest that comparing these rates cannot assess the optimality of behaviour when organisms are collecting F4G because the rate of resource use during this activity will be constrained by their ability to obtain metabolic fuel. Thus, although organisms may sometimes maximize a surrogate currency when obtaining non-energetic resources such as pollen (Rasheed and Harder, 1997), our models predict that such results will not be robust to changes in a forager's access to fuel.

Second, the accuracy with which a classical optimal foraging model will explain foraging for growth-enriching resources should depend on the ratio of fuel to F4G availability. Unlike classical foraging models, our fuel and F4G models assume that the relative rates of fuel and F4G intake are important, even if the overall rate of resource gain is unchanged.

Relative rates of intake affect foraging for F4G and defence because resource use is influenced by the rate of fuel intake, while the amount of resources collected is determined by the rate of F4G gain. Factors that increase relative rates of intake, such as the ratio of fuel to F4G availability, favour higher fuel use per unit of F4G acquired. Our work suggests that classical models underestimate the optimal tempo of foraging and optimal allocation to defence for omnivores in fuel-rich environments and for specialists on fuel-rich foods.

In addition to the nutritional effects described by our fuel and F4G models, several other factors may explain foraging behaviours that do not maximize the net rate of energy gain. Predation risk can cause foragers to forego feeding opportunities or invest more in vigilance, leading to strategies that are costlier than rate-maximizing solutions (Sih, 1980; Lima *et al.*, 1985; Nonacs and Dill, 1990; Brown, 1999). In contrast, when risk or damage increases with activity rate, foragers may choose tactics that are more efficient than those that maximize net intake rate (Schmid-Hempel *et al.*, 1985; McLaughlin and Montgomerie, 1990). Similarly, limits on feeding and assimilation capacities can favour strategies that maximize energetic efficiency rather than net intake rate (Ydenberg and Hurd, 1998).

Some models have predicted that behaviour also may not maximize net energy gain when foragers collect both provision for their young and resources for themselves (Houston, 1986, 1987, 1995; Waite and Ydenberg, 1994; Ydenberg *et al.*, 1994; Hedenström and Alerstam, 1995; McNamara and Houston, 1997; Welham and Beauchamp, 1997). As in our provisioning version of the tempo model, these models assume that foragers maximize the rate at which they deliver resources to the nest subject to meeting their own requirements for those resources. Ydenberg *et al.* (1994) predicted that a forager's rate of work while provisioning will increase with its net self-feeding rate and that provisioning behaviour will only maximize the net rate of energy intake when its rate of self-feeding is high. In contrast, our provisioning model predicts that foragers will maximize net energy intake rate even when they are collecting resources for their young. Our provisioners are predicted to forage at the same tempo as foragers feeding themselves because they both are seeking to maximize the acquisition of excess energy in a given amount of time.

Previous models that distinguished between self-feeding and provisioning assumed that obtaining resources for activity and for growth are distinct processes; thus, these models resemble the fuel and F4G version more than the provisioning version of our tempo model. Our assumption that foragers use fuel to maximize F4G gain is analogous to foragers self-feeding to maximize delivery rates, and our prediction that the tempo of foraging for F4G increases with the net rate of fuel acquisition is analogous to optimal provisioning rates increasing with the net rate of self-feeding. The key difference between our model and previous provisioning models is that our model assumes that foraging for fuel and for provision are distinct processes because fuel and F4G are different resources. In the model of Ydenberg *et al.* (1994), rates of self-feeding and provisioning are strategic decisions made by foragers. In contrast, the relative rates of fuel acquisition and F4G acquisition in our model are influenced by the availabilities of these resources in the environment. This distinction allows our model to predict the environmental circumstances that will favour high-tempo provisioning behaviour.

Few data are available to test the predictions of the fuel and F4G models, although anecdotal evidence suggests their relevance. Several social insects supplement diets of protein-rich animal tissue with plant and homopteran exudates. These exudates qualify as fuels because they are rich in carbohydrates, but they are poor in protein and other nutrients essential for growth (Hölldobler and Wilson, 1990). Davidson (1997) noted that tropical

arboreal ant species with easy access to these exudates often have 'rapid or even frenzied activity' (p. 163) levels and tend to aggressively defend territories from intrusion. Although access to exudates and differences in tempo and territoriality remain to be quantified and compared, these observations suggest that interspecific differences in tempo and aggressiveness may reflect differences in the qualitative characteristics of available resources.

The tempo and defence models may also explain the responses of animals to diets that are nutritionally imbalanced. Both mammals and insects have been found to increase metabolic rates when fed diets that are richer in carbohydrates but poorer in protein relative to their preferred diets (Trier, 1996; Zanotto *et al.*, 1997). This increase in metabolic rate has been interpreted as a mechanism for removing excess carbohydrates to maintain an optimal internal balance of nutrients (Trier, 1996; Raubenheimer and Simpson, 1997; Zanotto *et al.*, 1997). However, in the field, high metabolic rates could also improve an animal's nutrient budget. For example, animals facing an over-abundance of carbohydrates or lipids could raise their tempo to increase the rate at which they acquire nutrient-rich resources (e.g. Boersma *et al.*, 2001; Boersma and Kreutzer, 2002), and could spend more time and effort protecting protein resources from competitors.

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REFERENCES

Belovsky, G.E. 1978. Diet optimization in a generalist herbivore: the moose. *Theor. Pop. Biol.*, **14**: 105–134.

Boersma, M. and Kreutzer, C. 2002. Life at the edge: is food quality really of minor importance at low quantities? *Ecology*, **83**: 2552–2561.

Boersma, M., Schöps, C. and McCauley, E. 2001. Nutritional quality of seston for the freshwater herbivore *Daphnia galeata x hyaline*: biochemical versus mineral limitation. *Oecologia*, **129**: 342–348.

Brown, J.S. 1999. Vigilance, patch use and habitat selection: foraging under predation risk. *Evol. Ecol. Res.*, **1**: 49–71.

Calow, P. and Townsend, C.R. 1981. Energetics, ecology and evolution. In *Physiological Ecology: An Evolutionary Approach to Resource Use* (C.R. Townsend and P. Calow, eds), pp. 3–19. Sunderland, MA: Sinauer Associates.

Carpenter, F.L. 1987. Food abundance and territoriality: to defend or not to defend? *Am. Zool.*, **27**: 387–399.

Carpenter, F.L. and MacMillen, R.E. 1976. Threshold model of feeding territoriality and test with a Hawaiian Honeycreeper. *Science*, **194**: 639–642.

Cottam, D.A. 1985. Frequency-dependent grazing by slugs and grasshoppers. *J. Ecol.*, **73**: 925–933.

Dadd, R.H. 1985. Nutrition: organisms. In *Comprehensive Insect Physiology, Biochemistry and Pharmacology* (G.A. Kerkut and L.I. Gilbert, eds), pp. 364–437. Oxford: Pergamon Press.

Davidson, D.W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biol. J. Linn. Soc.*, **61**: 153–181.

Davies, N.B. and Houston, A.I. 1981. Owners and satellites: the economics of territory defence in the pied wagtail, *Motacilla alba*. *J. Anim. Ecol.*, **50**: 157–180.

Davies, N.B. and Houston, A.I. 1984. Territory economics. In *Behavioural Ecology: An Evolutionary Approach* (J.R. Krebs and N.B. Davies, eds), pp. 148–169. Sunderland, MA: Sinauer Associates.

Dyer, F.C. and Seeley, T.D. 1991. Nesting behavior and the evolution of worker tempo in four honey bee species. *Ecology*, **72**: 156–170.

Franks, N.R. 1985. Reproduction, foraging efficiency and worker polymorphism in army ants. In *Experimental Behavioral Ecology and Sociobiology* (B. Hölldobler and M. Lindauer, eds), pp. 91–107. Sunderland, MA: Sinauer Associates.

Hedenström, A. and Alerstam, T. 1995. Optimal flight speed of birds. *Phil. Trans. R. Soc. Lond. B*, **348**: 471–487.

Hölldobler, B. and Wilson, E.O. 1990. *The Ants*. Cambridge, MA: Belknap Press.

Houston, A.I. 1986. The optimal flight velocity for a bird exploiting patches of food. *J. Theor. Biol.*, **119**: 345–362.

Houston, A.I. 1987. Optimal foraging by parent birds feeding dependent young. *J. Theor. Biol.*, **124**: 251–274.

Houston, A.I. 1995. Energetic constraints and foraging efficiency. *Behav. Ecol.*, **6**: 393–396.

Kacelnik, A., Houston, A.I. and Krebs, J.R. 1981. Optimal foraging and territorial defence in the great tit. *Behav. Ecol. Sociobiol.*, **8**: 35–40.

Leonard, J.G. and Herbers, J.M. 1986. Foraging tempo in two woodland ant species. *Anim. Behav.*, **34**: 1172–1181.

Lima, S.L., Valone, T.J. and Caraco, T. 1985. Foraging-efficiency–predation-risk trade-off in the grey squirrel. *Anim. Behav.*, **33**: 155–165.

Maher, C.R. and Lott, D.F. 1995. Definitions of territoriality used in the study of variation in vertebrate spacing systems. *Anim. Behav.*, **49**: 1581–1597.

McLaughlin, R.L. and Montgomerie, R.D. 1990. Flight speeds of parental birds feeding nestlings: maximization of foraging efficiency or food delivery rate? *Can. J. Zool.*, **68**: 2269–2274.

McNamara, J.M. and Houston, A.I. 1997. Currencies for foraging based on energetic gain. *Am. Nat.*, **150**: 603–617.

Nonacs, P. and Dill, L.M. 1990. Mortality risk vs. food quality trade-offs in a common currency: ant patch preferences. *Ecology*, **71**: 1886–1892.

Oster, G.F. and Wilson, E.O. 1978. *Caste and Ecology in the Social Insects*. Princeton, NJ: Princeton University Press.

Pennings, S.C., Nadeau, M.T. and Paul, V.J. 1993. Selectivity and growth of the generalist herbivore *Dolabella auricularia* feeding upon complementary resources. *Ecology*, **74**: 879–890.

Perrin, N. and Sibly, R.M. 1993. Dynamic models of energy allocation and investment. *Annu. Rev. Ecol. Syst.*, **24**: 379–410.

Pulliam, H.R. 1975. Diet optimization with nutrient constraints. *Am. Nat.*, **109**: 765–768.

Pyke, G.H. 1981. Optimal travel speeds of animals. *Am. Nat.*, **118**: 475–487.

Rapport, D.J. 1980. Optimal foraging for complementary resources. *Am. Nat.*, **116**: 324–346.

Rasheed, S.A. and Harder, L.D. 1997. Foraging currencies for non-energetic resources: pollen collection by bumblebees. *Anim. Behav.*, **54**: 911–926.

Raubenheimer, D. and Simpson, S.J. 1997. Integrative models of nutritional balancing: application to insects and vertebrates. *Nutr. Res. Rev.*, **10**: 151–179.

Schmid-Hempel, P., Kacelnik, A. and Houston, A.I. 1985. Honeybees maximize efficiency by not filling their crop. *Behav. Ecol. Sociobiol.*, **17**: 61–66.

Shaw, J.J., Tregenza, T., Parker, G.A. and Harvey, I.F. 1995. Evolutionary stable foraging speeds in feeding scrambles: a model and an experimental test. *Proc. R. Soc. Lond. B*, **260**: 273–277.

Sih, A. 1980. Optimal behavior: can foragers balance conflicting demands? *Science*, **210**: 1041–1043.

Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.

Stephens, D.W. and Krebs, J.R. 1986. *Foraging Theory*. Princeton, NJ: Princeton University Press.

Trier, T.M. 1996. Diet-induced thermogenesis in the prairie vole, *Microtus ochrogaster*. *Physiol. Zool.*, **69**: 1456–1468.

Waite, T.A. and Ydenberg, R.C. 1994. Shift towards efficiency-maximizing by grey jays hoarding in winter. *Anim. Behav.*, **48**: 1466–1468.

Ware, D.M. 1975. Growth, metabolism, and optimal swimming speed of a pelagic fish. *J. Fish. Res. Board Can.*, **32**: 33–41.

Welham, C.V.J. and Beauchamp, G. 1997. Parental provisioning in a variable environment: evaluation of three foraging currencies and a state variable model. *Evol. Ecol.*, **11**: 399–417.

Ydenberg, R. and Hurd, P. 1998. Simple models of feeding with time and energy constraints. *Behav. Ecol.*, **9**: 49–53.

Ydenberg, R., Welham, C.V.J., Schmid-Hempel, R., Schmid-Hempel, P. and Beauchamp, G. 1994. Time and energy constraints and the relationships between currencies in foraging theory. *Behav. Ecol.*, **5**: 28–34.

Zanotto, F.P., Gouveia, S.M., Simpson, S.J., Raubenheimer, D. and Calder, P.C. 1997. Nutritional homeostasis in locusts: is there a mechanism for increased energy expenditure during carbohydrate overfeeding? *J. Exp. Biol.*, **200**: 2437–2448.